



Evapotranspiration from a Mediterranean evergreen oak savannah: The role of trees and pasture

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SUMMARY

Mediterranean evergreen oak woodlands of southern Portugal (*montados*) are savannah-type ecosystems with a widely sparse tree cover, over extensive grassland. Therefore, ecosystem water fluxes derive from two quite differentiated sources: the trees and the pasture. Partitioning of fluxes according to these different sources is necessary to quantify overall ecosystem water losses as well as to improve knowledge on its functional behaviour. In southern Iberia, these woodlands are subjected to recurrent droughts. Therefore, reaction/resilience to water stress becomes an essential feature of vegetation on these ecosystems. Long-term tree transpiration was recorded for 6 years from a sample of holm oak (*Quercus ilex* ssp. *rotundifolia*) trees, using the Granier sap flow method. Ecosystem transpiration was measured by the eddy covariance technique for an 11-month period (February to December 2005), partly coincident with a drought year. Pasture transpiration was estimated as the difference between ecosystem (eddy covariance) and tree (sap flow) transpiration. Pasture transpiration stopped during the summer, when the surface soil dried up. In the other seasons, pasture transpiration showed a strong dependence on rainfall occurrence and on top soil water. Conversely, trees were able to maintain transpiration throughout the summer due to the deep root access to groundwater. *Q. ilex* trees showed a high resilience to both seasonal and annual drought. Tree transpiration represented more than half of ecosystem transpiration, in spite of the low tree density (30 trees ha⁻¹) and crown cover fraction (21%). Tree evapotranspiration was dominated by transpiration (76%), and interception loss represented only 24% of overall tree evaporation.

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Introduction

Mediterranean evergreen oak woodlands, called *montados* in Portugal and *dehesas* in Spain, represent 33% of the total Portuguese forested area. They have a sparse tree cover, over native grassland (or a dryland grown pasture) that recurrently develops into a shrubland. They are mainly located in areas of southern Portugal and Spain with a Mediterranean climate. In these areas, evaporative demand is higher than annual rainfall and the dry season (summer) lasts for several months. Natural droughts are recurrent. Drought severity is increasing and can be further aggravated due to climate change and human action (Isendahl and Schmidt, 2006; Miranda et al., 2006). Therefore, the response of these Mediterranean oak woodlands to water stress is an important issue. Also, the quantification of evapotranspiration from these ecosystems is critical for a correct evaluation of the scarce local water resources.

However, this is not a simple task since these are savannah-type ecosystems composed by two quite different plant life forms: the trees and the grassland (Joffre and Rambal, 1993; Baldocchi et al., 2004; Baldocchi and Xu, 2007). Therefore, the whole ecosystem cannot be considered as a single, spatially uniform layer for carbon or water vapour exchange with the atmosphere. A two-source approach will certainly be more appropriated. Furthermore, the different life forms are quite variable regarding water use, with deep rooted evergreen trees and shallow rooted malacophyllous shrubs and annual grasses. Tackling changes in water use by two layered ecosystems may increase in complexity as the plant functional type diversity increases due to differences in phenology and rooting depth of plant species (Pereira et al., 2006). The partitioning of ecosystem evapotranspiration between plant life forms and according to different sources is necessary to quantify and model the overall ecosystem water losses as well as to improve the understanding on its functional behaviour.

Partitioning of ecosystem fluxes have been attempted in other studies, whether for carbon dioxide (e.g., Baldocchi and Vogel,

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1996; Kelliher et al., 1999; Law et al., 2001; Falk et al., 2005), water (e.g., Brunel et al., 1997; Baldocchi et al., 2000, 2004; Williams et al., 2004; Lauenroth and Bradford, 2006; Scott et al., 2006) or both (e.g., Constantin et al., 1999; Lamaud et al., 2001; Wilson and Meyers, 2001). Water flux partitioning can be addressed by several approaches, although most frequently the eddy covariance technique is involved as a direct way of estimating evapotranspiration at the ecosystem level. In woody stands, the eddy covariance technique may be combined with tree sap flow measurements to separately estimate tree and ecosystem evaporation (e.g., Köstner et al., 1992; Hutley et al., 2001; Mackay et al., 2002; Silva et al., 2008). Understorey evaporation can be estimated from the difference between eddy covariance and sapflow measurements or directly measured. Direct assessment of understorey evaporation is sometimes done by the eddy covariance or exchange chamber techniques (e.g., Daudet, 1987; Loustau and Cochard, 1991; Améglio et al., 1993). The use of the eddy covariance method below tree canopy may not respect its theoretical assumptions (Misson et al., 2007), but some authors showed that it can be used after a thorough validation of measurements (e.g. Baldocchi et al., 2000; Lamaud et al., 2001; Wilson and Meyers, 2001).

This work aims at a better understanding of evapotranspiration from a *Quercus ilex* (holm oak) savannah-type ecosystem (*montado*), by studying the contribution of its two components: the trees and the herbaceous vegetation. Tree transpiration was measured continuously for 6 years (2001–2006) using a sap flow method (*Granier* method). These data allowed the analysis of inter-annual variation of tree transpiration, including extreme drought conditions. Indeed, during the measuring period an extremely severe drought occurred in 2004 and 2005. This was the most severe drought in the last 60 years in terms of affected land area (EEA, 2007). Eddy covariance measurements at the ecosystem level were carried out in 2005 (11-month period). The herbaceous transpiration was estimated for that period as the simple difference between ecosystem transpiration (eddy covariance) and tree transpiration (sap flow).

Tree canopies always intercept a substantial proportion of the rainfall which is either evaporated – interception loss – or reaches the ground as stemflow or throughfall (Ward and Robinson, 2000). Interception loss is usually an important component of tree evapotranspiration since, under similar weather conditions (radiation and vapour pressure deficit), evaporation rate from a wet tree canopy is much higher than the corresponding transpiration rate, due to a very low aerodynamic resistance (Rutter, 1975; David et al., 2005). In short vegetation, the aerodynamic resistance is one order of magnitude higher than in forests and the evaporation rate from wet leaves is about the same of transpiration rate for similar radiation and humidity (Rutter, 1975; David et al., 2005). This is why the evaporation of intercepted rainfall is a net loss in trees, but not so in short vegetation. Therefore, interception loss was only considered for the tree component of the studied ecosystem, being evaluated through the tree-based adaptation of Gash's analytical model described by Pereira et al. (2009a).

Materials and methods

The experimental site and meteorology

The experimental site is a sparse, savannah-type evergreen holm oak (*Q. ilex* ssp. *rotundifolia* Lam.) *montado*, located at Herdade da Alfaroibeira, near Évora, Portugal, hereafter referred to as Mitra II (38°32'N, 8°00'W, 256 m a.s.l.). Site topography is slightly undulating. The climate is Mediterranean, with mild, wet winters and hot, dry summers. Long-term average annual rainfall is around 669 mm and mean air temperature around 15 °C. Mean stand den-

sity is around 30 trees ha⁻¹ and tree crown cover about 21% (Carreiras et al. 2006). The trees have mean trunk diameter at breast height, crown projected area and height of 0.34 (±0.17) m, 69 m² and 8 m, respectively. The short vegetation between and beneath the trees is a natural pasture composed mainly of annual graminiae (such as *Vulpia bromoides* (L.) S.F. Gray and *Avena barbata* Link), legumes (such as *Ornithopus compressus* L. and *Trifolium subterraneum* L.) and forbs (such as *Tuberaria guttata* (L.) Fourr), with a few intermingled shrubs (mainly *Cistus salviifolius*, L.). The soil is a ca. 1 m deep Dystric Cambisol (FAO, 1988), overlying granite bedrock.

Meteorological measurements were performed at the site throughout the experimental period (2001–2006). Wind speed (anemometer A100R, Vector Instruments, Rhyl, UK) and direction (wind vane W200P, Vector Instruments, Rhyl, UK), air temperature and humidity (aspirated psychrometer H301, Vector Instruments, Rhyl, UK), solar radiation (CM6B, Kipp and Zonen, Delft, The Netherlands) and net radiation (Q7, REBS, Seattle, USA) were measured at the top of a 28-m-high tower (about 20 m above tree canopy). Rainfall was measured at ground level with a tipping-bucket rain gauge (ARG100, Environmental Measurements, Gateshead, UK). Data were stored in a CR10X data logger (Campbell Scientific, Shepshed, UK) at 10-min intervals.

Sap flow measurements

Sap flow was measured in four *Q. ilex* trees from 2001 to 2006, using the *Granier* method (Granier, 1985, 1987) in order to estimate tree transpiration. Mean diameter at breast height (*DBH*) of sampled trees was 0.38 m. These trees were randomly selected from a larger group ($n = 20$) with mean *DBH* of 0.34 (±0.17) m. One sap flow sensor (2 cm long) was installed in the south-facing xylem of each sampled tree. Sap flow sensors were replaced only in case of disruption, since it has been shown that probes do not deteriorate with time and are reliable for long-term measurements in this species (David et al., 2004). Sapwood conductive thickness was estimated from the sap flow radial profile obtained by the heat field deformation method (Nadezhdina et al., 1998) in two *Q. ilex* trees. Tree sap flow was calculated as the product of sap flow density (measured by the *Granier* probes) and sapwood conductive area. Average sap flow of the oak stand was estimated as the mean of the four sampled trees. For further details of sap flow measurements and assumptions see David et al. (2007). Sap flow data were integrated on a daily basis and considered equal to tree transpiration at this time-scale. Tree transpiration was expressed in mm day⁻¹ per unit of crown projected area. For comparisons with total ecosystem transpiration (eddy covariance data), transpiration values on a crown area basis were converted into a ground area basis, in mm day⁻¹, multiplying by the tree crown cover fraction (0.21).

Tree canopy conductance

Sap flow measurements (per unit of crown projected area) were used to derive midday tree canopy conductance (g_c), using the approximation of McNaughton and Jarvis (1983) and Jarvis and McNaughton (1986) for vegetation highly-coupled to the atmosphere (see David et al., 2007):

$$T_t = g_c D_e \frac{\rho c_p}{\lambda \gamma} \quad (1)$$

where T_t is tree transpiration (kg m⁻² s⁻¹), g_c is canopy conductance (m s⁻¹), D_e is the vapour pressure deficit of the air (Pa), λ is latent heat of evaporation of water (J kg⁻¹), γ is the psychrometric constant (Pa °C⁻¹), ρ is the density of air (kg m⁻³) and c_p is the heat capacity of water in air (J kg⁻¹ °C⁻¹). Midday canopy conductance

was calculated during selected months of the drying-up season (April, June, August and October) of the driest (2005) and the wettest (2001) years of the recording period. Days with rainfall were discarded and g_c values were expressed in mm s^{-1} , per unit of crown projected area.

The sensitivity of g_c response to D_e was studied using the approach developed by Oren et al. (1999) using the equation:

$$g_c = b - m \ln D_e \quad (2)$$

where the parameters m and b are generated by least-square regression analysis. The parameter m quantifies the sensitivity of g_c (mm s^{-1}) to D_e (kPa) and b is a reference conductance at $D_e = 1$ kPa. Theoretically, the ratio m/b will approach 0.6 as long as stomata are regulating efficiently leaf water potential towards a constant value. If the ratio drops below that value, there is a lack of response of stomata to changes in leaf water potential and some degree of xylem cavitation occurs (Oren et al., 1999).

Groundwater table

The depth of water table was monitored from 2002 to 2005 in a 20-m-deep borehole by a pressure transducer (PDCR 830, Campbell Scientific, Shepshed, UK). The pressure transducer measures the difference in pressure between the atmosphere and that at the depth of the sensor. Since this type of sensor only measures accurately water heights up to 3.60 m, its position was changed periodically to cover the all annual range of water table level variation. Usually two positions per year were enough: one at about 3.5 m below soil surface during the wet season (from late autumn to early spring) and another at about 6 m depth during the remainder of the year (dry season). The borehole was dug down near the sampled *Q. ilex* trees. Data were stored at 10-min intervals in a CR10X data logger.

Rainfall interception loss from trees

Interception loss from *Q. ilex* trees was estimated using a tree-based adaptation of the *Gash* analytical model, as described by Pereira et al. (2009a). The crown of each isolated tree was considered as a closed canopy and interception loss calculated on a crown area basis. In this case we could use either the revised, sparse (Gash et al., 1995), or the original version (Gash, 1979) of the *Gash* model, since they are almost equivalent when canopy cover (c) is 100% ($c = 1$). The use of the sparse version was, however, preferred since its formulation is free from some of the conceptual errors of the original version (Valente et al., 1997).

The *Gash* model assumes that rainfall is a succession of discrete events, with sufficient time between them for the canopy and trunks to dry-up completely. The canopy and trunks are described by a set of structural parameters, such as the canopy storage capacity (S) and the canopy cover fraction (c). The actual rates of rainfall and maximum possible evaporation are replaced by average values of these variables (\bar{R} and \bar{E} , respectively). We used two of the model parameters derived by Pereira et al. (2009a,b) for *Q. ilex* trees: crown storage capacity ($S = 1.16$ mm) and average evaporation rate during saturated conditions ($\bar{E} = 0.27$ mm h^{-1}). Average hourly rainfall rate \bar{R} was calculated from all hours when rainfall exceeded a certain threshold (0.4 mm), following the procedure used by Gash (1979) and Pereira et al. (2009a): $\bar{R} = 1.82$ mm h^{-1} .

The model was successfully tested against measurements in *Q. ilex* trees by Pereira et al. (2009a): modelling estimates were within an error band of 9% from observations.

Model calculations are performed hourly but integration of final output is done daily: rain that falls on a day is assumed as a single storm. Further details on the modelling conceptual background,

parameter derivation and modelling performance are given by Pereira et al. (2009a,b).

Eddy covariance measurements

Eddy covariance measurements of latent and sensible heat were performed from February to December 2005, using an ultrasonic anemometer (Solent R3 Gill Instruments, Ltd., Hampshire, UK) and a closed-path IRGA (LI-7000 LI-COR, Lincoln, Nebraska, USA). The instruments were placed above the top of the metallic tower, at a height of 29 m, as described in Pereira et al. (2007). A combined footprint and quality assessment analysis was performed under different stability conditions, as described in Göckede et al. (2004, 2008). According to the Göckede et al. (2008) assessment criteria, data quality for latent heat flux was moderate and the fetch conditions were perfect (the measured flux had an average flux contribution from the target area of 99%). Methods used in flux data processing and computation are described in more detail by Pereira et al. (2007). Data collected during rain were considered unreliable.

Water flux measurements were used to assess total ecosystem transpiration, discarding rainy days (thus excluding days with rainfall interception) and considering soil evaporation negligible. The assumption of negligible soil evaporation is supported on three main reasons: (a) the typically small number of rainfall events that characterize local climate: long-term average (1951–1980) of rain days per year is 85 (INMG, 1991); (b) the sandy nature of the surface soil, with a very low water retention capacity; and (c) the shelter effect of short vegetation during the wet season on radiation and wind speed.

Transpiration data was stored in a PC at half-hourly intervals and integrated on a daily basis. Daily transpiration was expressed in mm day^{-1} , per unit of ground area.

Transpiration from pasture

Daily pasture transpiration was estimated as the difference between total daily ecosystem transpiration (eddy covariance) and daily tree transpiration (sap flow). All variables were expressed on the same reference area basis: per unit of ground area. Calculations were performed only for rainless days, during 2005, when eddy covariance data were available.

Results and discussion

Long-term tree transpiration

Fig. 1 shows the long-term trend of daily tree transpiration measured by sap flow, along with solar radiation (A), groundwater table depth (B) and rainfall (C and D), for the 2001–2006 period. Annual rainfall was higher than the long-term average (1961–1990, 669 mm) in 2001, 2002, 2003 and 2006 and lower in 2004 and 2005 (Fig. 1D). The wettest year of the record was 2001 and the driest 2005. A 2-year drought period occurred during 2004 and 2005, with the peak of drought severity in the second year. Annual rainfall in 2004 and 2005 was only 73% and 64% of the long-term local average, respectively (Fig. 1D and Fig. 2) and winter rainfall in 2005 was only 12% of the long-term mean. During normal or wet years (2001–2003 and 2006), transpiration showed a trend following closely radiation till the end of spring, when a maximum occurred (this maximum was reached by the middle of June, in all years) (Fig. 1A). After that, transpiration became off-set behind the radiation trend, showing a progressive decrease during the summer and a recovery upon the onset of autumn rains.

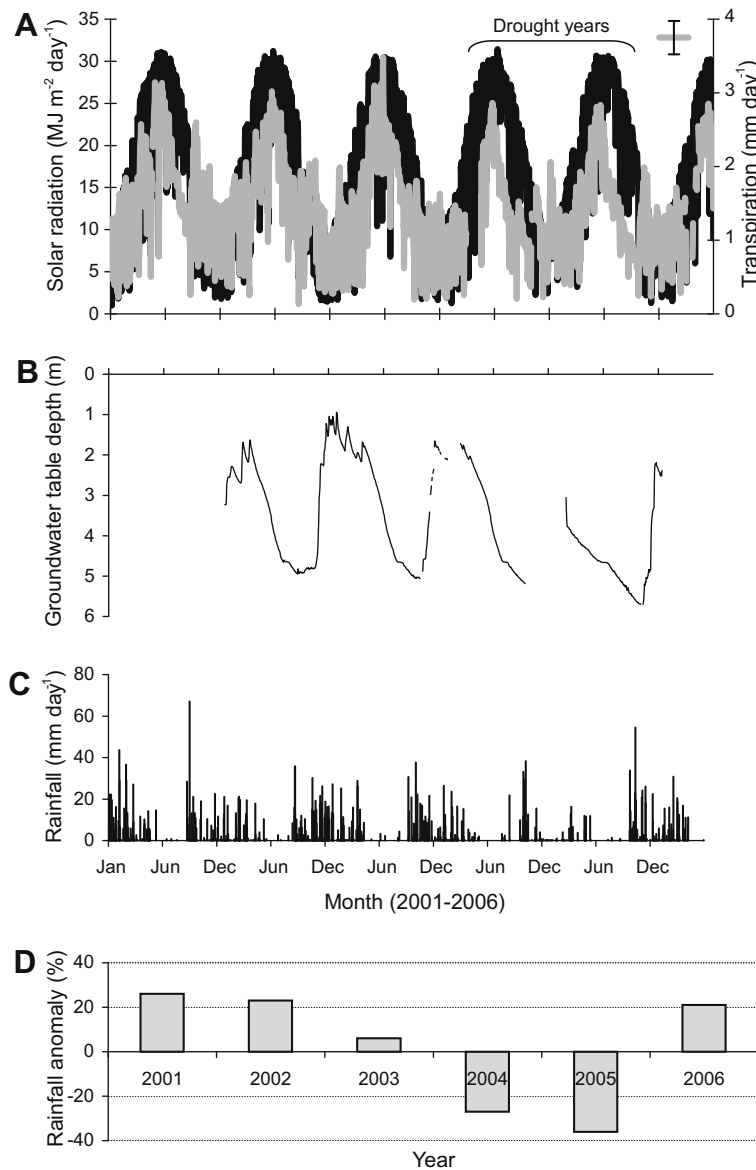


Fig. 1. Long-term evolution of (A) daily tree transpiration (*Quercus ilex*, $n = 4$) per unit of crown projected area (T_r , grey line) and solar radiation (black line) and (B) and (C) other environmental variables (B – groundwater table depth and C – rainfall), from 2001 to 2006. Rainfall anomaly to long-term annual average (669 mm, 1961–1990) is also represented (D). In (A) the error bar is the average standard error of tree transpiration.

In the drought years (2004 and 2005) the maximum transpiration rate was lower and occurred earlier than in normal/wet years.

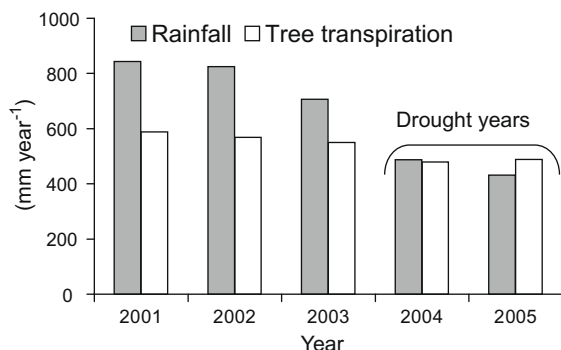


Fig. 2. Annual rainfall and tree transpiration (per unit of crown projected area) for the 2001–2005 period.

Moreover, the summer depression in transpiration lasted longer in the dry years (Fig. 1A), which means a more severe summer water stress than in normal/wet years. Nevertheless, clear sky daily tree transpiration never fell below a minimum of 0.6 mm day⁻¹ (Fig. 1A), and the drop of annual tree transpiration in the drought years was of only ca. 16% (Fig. 2). This relative decline in annual transpiration during drought was much smaller than the corresponding variation in annual rainfall (Fig. 2), evidencing a high resilience of the trees throughout the 2-year successive drought.

Fig. 2 shows that the proportion of rainwater used by the trees increases as the drought progresses, as also found by Zeppel et al. (2008). The high resilience of the trees during drought can probably be ascribed to the direct, permanent access of roots to the local groundwater reservoir. In summer 2002, stable isotope (deuterium) analyses in xylem, soil and groundwater at the site, showed that groundwater withdrawal accounted for more than 70% of total tree transpiration (David et al., 2007). This is not surprising, since it is known that evergreen trees in semi-arid environments, with seasonal drought, often rely on deep rooting and on the ability to tap

water from permanent water tables (e.g., Walter 1973; Canadell et al., 1996; Le Maitre et al., 1999; Lubczynski and Gurwin, 2005; Schenk and Jackson, 2005; David et al., 2004, 2007), frequently showing an appreciable degree of decoupling relative to rainfall (e.g. Scott et al., 2003; Yezpez et al., 2003). However, to our knowledge, this is the longest sap flow dataset ever published showing this high resilience of Mediterranean trees to prolonged drought.

Root access to groundwater will depend on tree rooting habits, water table depth and bedrock characteristics. Water table depth at our site varied between 1–2 m in winter and around 5 m in summer, in normal/wet years. Summer water table depth increased slightly during the drought, reaching a maximum of 5.8 m in the summer of 2005 (Fig. 1B). The hard nature of the bedrock at the experimental site (granite) probably somehow limited the development and the number of effective deep tap roots. In more fractured bedrocks, deep root development will certainly be facilitated. At a nearby site (Mitra I), where the bedrock was a fractured gneiss and water table depth around 13 m, David et al. (2004) found a very efficient access of *Q. ilex* roots to groundwater, which allowed transpiration to follow the radiation trend all year around without any signs of summer water stress. Fig. 3 compares tree transpiration, predawn leaf water potential (Ψ_p) and cumulative rainfall obtained during 2002 at our site (Mitra II) (David et al., 2007) to similar data for the same species (*Q. ilex*) collected by David et al. (2004) at the nearby Mitra I site in 1997. In both years, rainfall was higher than long-term average (54% and 24% for 1997 and 2002, respectively), mainly due to heavy autumn rains.

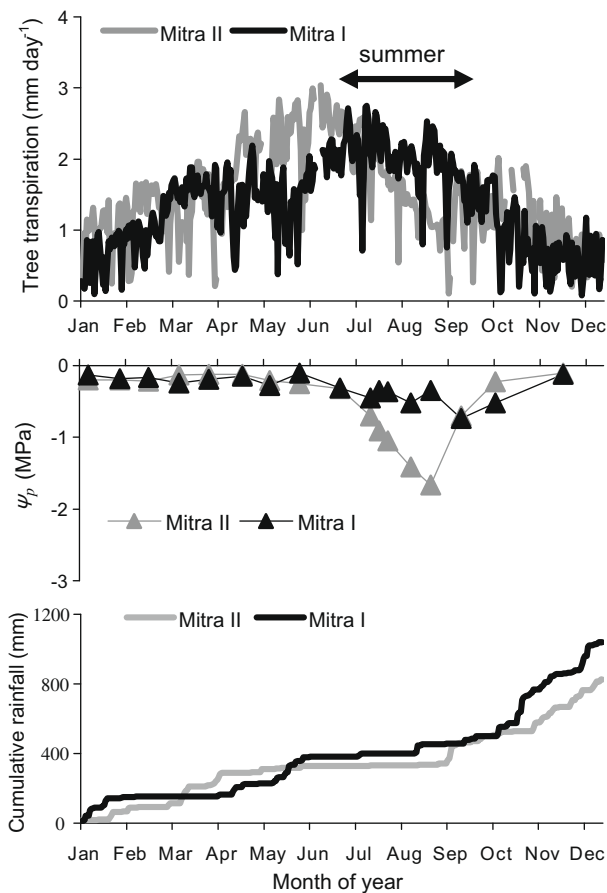


Fig. 3. Annual trends of *Q. ilex* transpiration (per unit of crown projected area), predawn leaf water potential (Ψ_p) and cumulative rainfall evidencing different possible patterns of root groundwater uptake during summer, at two nearby sites: Mitra II, 2002 – the site under study – and Mitra I, 1997 (adapted from David et al., 2004, 2007).

Cumulative rainfall up to the end of the summer as well as summer precipitation did not differ much between the 2 years. The biggest deviation from complete similarity between the two summers was the occurrence of one isolated convective storm in 14 August 1997 in Mitra I. However, the effect of that storm on transpiration and Ψ_p was certainly short-lived, since the low water retention capacity (24 mm) of the shallow soil depletes in about 8 days, at the summer rates of tree transpiration (ca. 3 mm day⁻¹ in Mitra I) (see David et al. (2004)). Therefore, we think that the differences in tree transpiration and Ψ_p shown in Fig. 3 during the summer are mainly due to different patterns of root groundwater uptake between sites: a decrease in both tree transpiration and Ψ_p was evident in Mitra II, but not in Mitra I. Patterns shown in Fig. 3 are typical of both sites, since they replicate in other years.

To better interpret the pattern of variation of tree transpiration in wet and dry years, canopy conductance was calculated by Eq. (1) for the months of the drying-up period (spring to summer) of the wettest (2001) and driest (2005) years of the record. Fig. 4 shows the relationships between midday canopy conductance (g_c) and vapour pressure deficit (D_e) for April, June, August and October of 2001 and 2005. Table 1 shows the corresponding monthly values of g_c sensitivity to D_e (m) and the reference g_c at $D_e = 1$ kPa (b), calculated from Eq. (2). For each of the examined years, the relationships in April and June were quite similar (Fig. 4), although the reference g_c (b) and g_c sensitivity to D_e (m) were slightly lower in the dry year (2005) (Table 1). In both years, g_c showed a significant drop during the peak of the dry season (August) (Fig. 4). However, this g_c decrease was more pronounced in the dry year (2005)

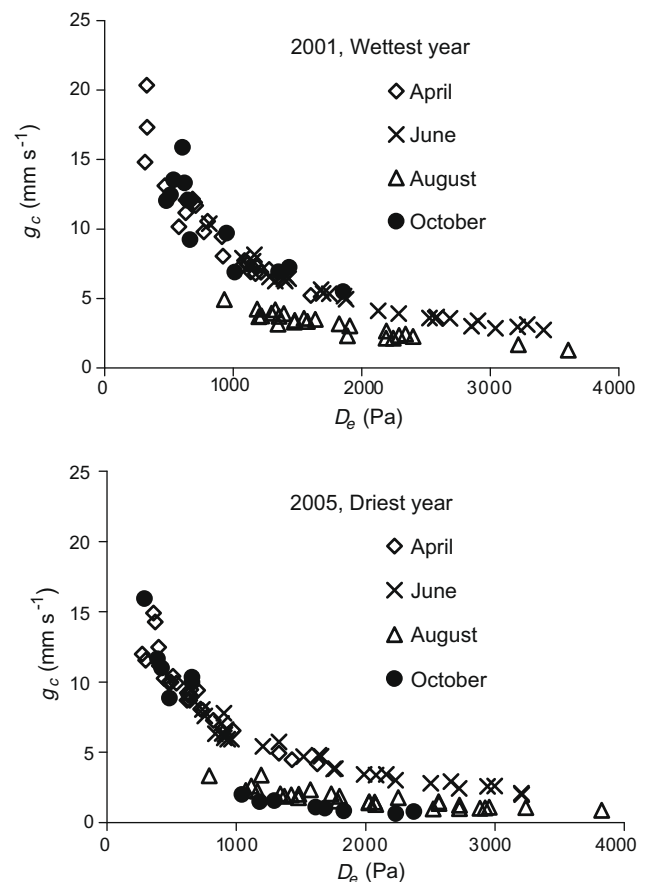


Fig. 4. Relationships between midday (12 h, UT time) canopy conductance (g_c) and vapour pressure deficit (D_e) for selected months (April, June, August and October), during the drying-up period of the wettest (2001) and driest (2005) years of the record.

Table 1

Values of the estimated parameters in Eq. (2) for some spring–summer months of 2001 and 2005; m is the sensitivity of g_c to D_e and b is the reference g_c (mm s^{-1}) at $D_e = 1$ kPa. Values of the m/b ratio are also shown.

	2001			2005		
	m	b	m/b	m	b	m/b
April	7.6	8.4	0.90	5.4	6.6	0.82
June	4.8	8.2	0.58	3.6	6.2	0.58
August	2.6	4.5	0.58	1.5	2.7	0.56
October	6.3	9.0	0.70	1.5 ^a	1.9 ^a	0.79 ^a

^a Values prior the g_c recovery in response to late October rain.

(Fig. 4), with lowest values of m and b (Table 1). This is in accordance with groundwater table data (Fig. 1B), which reached the lowest depth in summer of 2005.

The onset of autumn rainfall was earlier in 2001 (September) than in 2005 (late October). As a result, the g_c vs. D_e relationship recovered to pre-summer patterns in October 2001, but not in October 2005 (Fig. 4, Table 1). In 2005, g_c remained low during most of October and only recovered by the end of the month, when autumn rain started (Fig. 4). At the peak of the dry season (August) the m/b ratio was very similar in both years (0.58 in 2001 and 0.56 in 2005) and close to the theoretical 0.6 value, referred by Oren et al. (1999). This means that stomata were efficiently regulating leaf water potential in summer, avoiding xylem embolism, even during the peak of the drought in 2005. These results emphasize again the high resilience of the *Q. ilex* trees to severe drought. In a Spanish *dehesa*, Infante et al. (2003) also observed a strong stomatal regulation in *Q. ilex*, which prevented significant variations in water loss and tree water relations during prolonged drought.

Tree interception loss and tree evapotranspiration

Rainfall interception by tree canopies and subsequent evaporation loss may reach an important proportion of annual evapotranspiration. Although not measured, interception loss from the trees (I) was estimated by the tree-based adaptation of the Gash analytical model (Pereira et al., 2009a,b). Fig. 5 shows the cumulative interception loss for 2001–2005, per unit of tree crown projected area. The figure also shows the cumulative values of tree transpiration (T_t , estimated by sap flow), tree evapotranspiration ($ET_t = T_t + I$) and rainfall (P), during the 5-year period. Interception loss was 27% of rainfall per unit of crown projected area (or 6% of P per unit of ground area) and 24% of tree evapotranspiration. These results agree well with interception loss measurements carried out in other isolated Mediterranean evergreen oaks. For instance, our estimate for the ratio of interception loss vs. rainfall (27%) is within

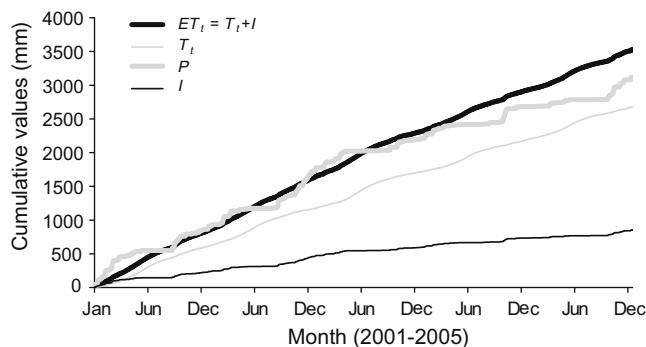


Fig. 5. Cumulative values of: I – interception loss; T_t – tree transpiration; ET_t – tree evapotranspiration ($T_t + I$) and P – rainfall (2001–2005). Values are expressed per unit of crown projected area.

the range of measured values for *Q. ilex* trees (22–30%) at nearby sites, Portugal (David et al., 2006; Pereira et al., 2009a), and for a *Q. suber* tree (27%) in California (Xiao et al., 2000). Likewise, the estimate for the ratio between interception loss and total tree evapotranspiration (24%) is close to that measured for a nearby *Q. ilex* tree (28%) (David et al., 2006). This agreement is consistent with the successful model validation performed by Pereira et al. (2009a) in isolated *Q. ilex* trees and reinforces the view that the tree-based adaptation of the Gash model is adequate to properly simulate the rainfall interception process in these Mediterranean evergreen oak savannahs. Gash and Stewart (1977), McNaughton and Jarvis (1983) and Shuttleworth (1988) report that interception loss from forests may vary from 25% to 75% of overall evaporation, depending on climate and forest type. Our values, as well as those of David et al. (2006) and Pereira et al. (2009a), are close to the lower limit of this interval, probably reflecting the rainfall distribution pattern of Mediterranean climate: a relatively small number of large storms. Although interception loss is a smaller component of tree evapotranspiration than transpiration, it must be taken into account and correctly evaluated since it represents about 24–28% of tree evapotranspiration.

Fig. 5 also shows that tree evapotranspiration (ET_t) is higher than precipitation (P) during the dry years of 2004 and 2005. This supports the earlier conclusion that deep tree roots are up taking a significant amount of water from the groundwater reservoir, causing the drop in the water table during the drought years shown in Fig. 1B.

Total ecosystem transpiration and its partitioning between trees and pasture

Fig. 6A represents the patterns of evolution of daily ecosystem transpiration (T_e , eddy covariance), tree transpiration (T_t , sap flow) and pasture transpiration ($T_p = T_e - T_t$) from February to December 2005, for rainless days. All values are expressed in the same reference area basis: per unit of ground area. Rainfall during the winter of 2005 was very low (Fig. 6B). However, the soil at the beginning of 2005 was wet, since the previous autumn (2004) had a significant amount of rain (237 mm, from October to December 2004, see Fig. 1C).

Data of Fig. 6 show that pasture transpiration (T_p) peaks in early spring (April), decreases thereafter till late spring, and stops by the beginning of July. During the summer (July–September) there is no transpiration from the pasture, and it only restarts after the onset of autumn rains (October). Tree transpiration peaks later (June), continues throughout the summer though decreasing progressively, and recovers upon autumn rainfall. During the summer drought (July–October) ecosystem transpiration equals tree transpiration, being pasture transpiration about zero. The continued transpiration of trees during summer is due to the resilience of evergreen oak trees to drought, as a result of deep rooting, as discussed above. During the dry summer season, pasture transpiration estimates show some small oscillations around an average close to zero ($0.003 \pm 0.08 \text{ mm day}^{-1}$). Residuals (deviations from the mean) are normally distributed (Shapiro–Wilk normality test, p -value = 0.22) around a mean zero value (2.8×10^{-10} , t test, p -value = 1) (Fig. 7). Therefore, pasture transpiration during the summer can be considered as approximately zero and oscillations around that are probably due to random instrumental errors. This also suggests that eddy covariance and sap flow measurements are both correct, since they coincided during the summer.

Whereas deep rooted trees behaved largely as drought avoiders tapping water from deep soil horizons or groundwater, the pasture shows a drought escaping behaviour (see Ludlow, 1989), with annual C3 herbaceous ceasing transpiration in summer when they stay in the form of seeds. Senescence of C3 herbs occurred by the

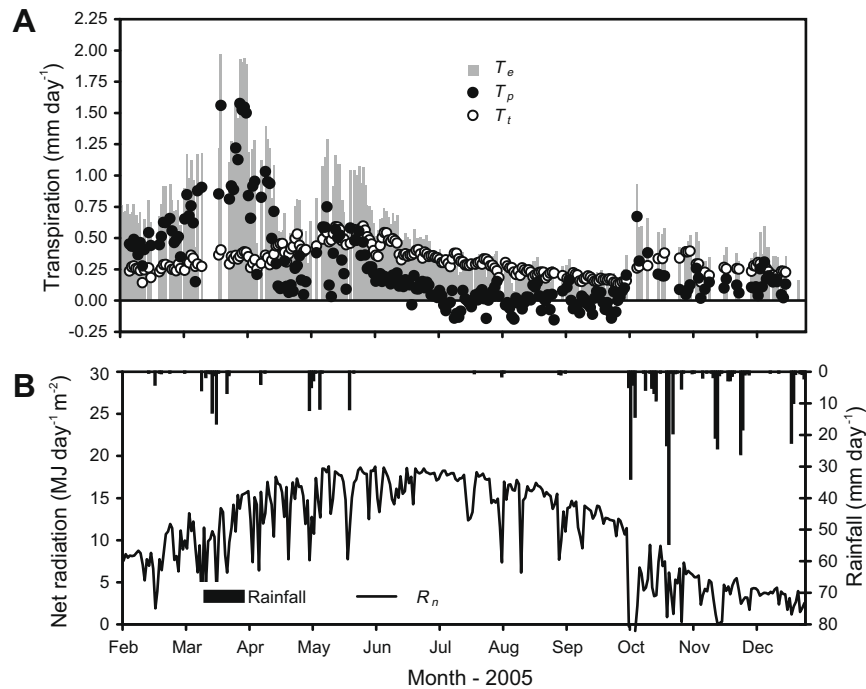


Fig. 6. (A) total ecosystem transpiration (T_e) and its partitioning between tree (T_t) and pasture (T_p) transpiration; (B) net radiation (R_n) and rainfall (from February to December 2005). All values are expressed per unit of ground area.

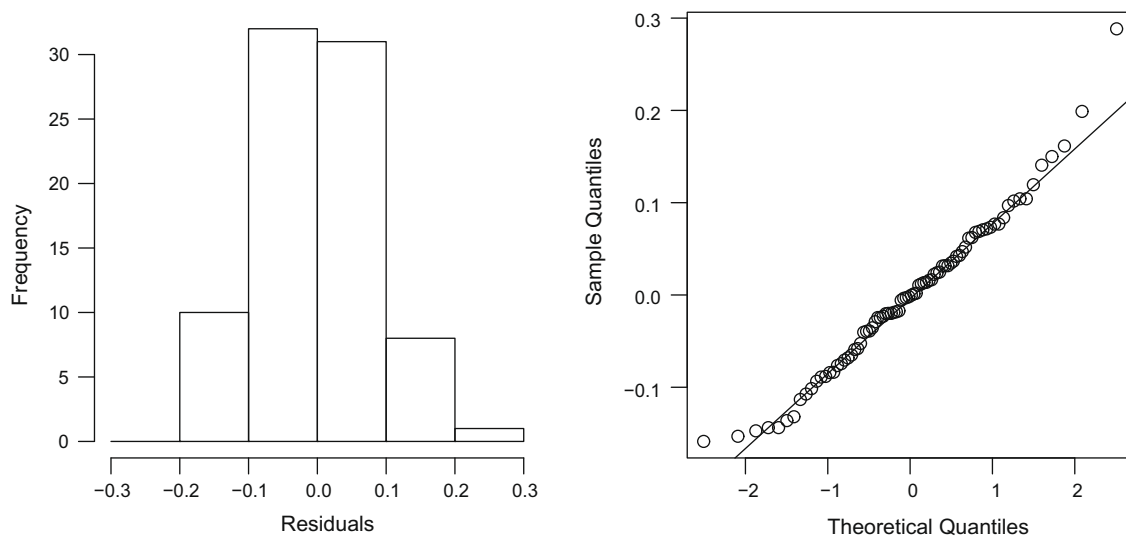


Fig. 7. Histogram and normal quantile–quantile plot of residuals calculated for pasture transpiration (T_p) during summer 2005, for the period DOY 194–281, when T_p approaches zero (mean = 0.003, standard deviation = 0.08).

beginning of May at a nearby open pasture studied by Aires et al. (2008). Pasture transpiration at our site stopped later (early July) probably due to the presence of scattered shrubs (*Cistus* spp.), the effect of hydraulically lifted water through tree roots (see David et al., 2007) and/or the tree shadow effect on below-crown vegetation (Joffre and Rambal, 1993; Ludwig et al., 2004). Nevertheless, the pasture seems coupled with near surface soil moisture, which depends on the occurrence of precipitation. Soil moisture content relative to field capacity (RWC) in the 0–20 cm soil layer was measured at the site by the gravimetric method, showing a decrease from 1 in winter to 0.1 in summer (Kurz-Besson, C. and David, T.S., 2007, personal communication). This dependence of herbaceous vegetation on top soil moisture was also

found by Joffre and Rambal (1993) in *Q. ilex dehesas* in southern Spain and by Baldocchi et al. (2004) in annual grassland in California, who report the same in phase behaviour.

The variation in the proportions of tree and pasture transpiration relative to overall ecosystem transpiration, for spring and summer 2005, showed that in spring the two sources equilibrate, with the pasture transpiration marginally higher (54%), but tree transpiration strongly dominates over pasture during the dry summer (90% and 10% of total, respectively). From February to December 2005, pasture and tree transpiration accounted for 44% and 56% of total ecosystem transpiration, respectively. The largest proportion of the ecosystem water use was, therefore, due to the trees (56%), although they only represent 21% of the ground cover.

Nevertheless, the contribution of pasture to total ecosystem transpiration found here (44%) is higher than that usually reported as typical for open forests (20–30% – Baldocchi and Xu, 2007).

Overall, our results on ecosystem flux partitioning totally agree with those obtained by Baldocchi et al. (2004) for a Californian oak savannah.

Concluding remarks

In the studied Mediterranean evergreen oak savannah, trees and pasture presented quite distinct behaviours regarding transpiration patterns. The pasture, mainly composed by annual herbs, was highly dependent on top soil water and very sensitive to summer drought: transpiration stopped in early summer. The trees were mostly dependent on deep soil and ground water, showing a high resilience to drought: transpiration continued throughout the summer, even though the canopy conductance decreased. Tree transpiration represented the highest proportion (56%) of total ecosystem transpiration, in spite of the low tree crown cover fraction (21%). Transpiration was the dominant component (76%) of overall tree evapotranspiration. Interception loss from trees represented only 24% of total tree evaporation. Reinforcing the conclusions already drawn by Baldocchi et al. (2004), our results show that the correct understanding and evaluation of water use by these savannah-type ecosystems can only be based on the separate, complementary analysis of its two components: the trees and the pasture.

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